

The Catfishes of the
Neotropical Family Helogenidae
(Ostariophysi: Siluroidei)

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and
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ABSTRACT

Vari, Richard P., and Hernán Ortega. The Catfishes of the Neotropical Family Helogenidae (Ostariophysi: Siluroidei). *Smithsonian Contributions to Zoology*, number 442, 20 pages, 9 figures, 3 tables, 1986.—The Neotropical catfish family Helogenidae is revised. Contrary to recent practice, a single genus *Helogenes* Günther is recognized, with *Leyvaichthys* Dahl treated as a synonym. Four species are recognized in the genus. *Helogenes marmoratus* Günther, an inhabitant of black and clearwater streams, is distributed throughout the Atlantic drainages of the Guianas and the upper Rio Orinoco of Venezuela, and within the Amazon basin has been collected in Venezuela, Brazil, Peru, and Ecuador. *Helogenes castaneus* (Dahl) is known only from the Rio Orinoco tributaries of eastern Colombia. *Helogenes uruyensis* Fernández-Yépez is evidently endemic to the vicinity of Auyantepui in the upper Rio Caroni, a southern tributary of the Rio Orinoco in southeastern Venezuela. *Helogenes gouldingi*, a previously unrecognized species, is described from a blackwater tributary of the Rio Madeira in Brazil.

Helogenes amazonae Delsman, described from an individual collected near Manaus, Brazil, and *H. unidorsalis* Glodek and Carter, based on specimens from eastern Ecuador, are considered synonyms of *H. marmoratus*. The presence or absence of an adipose dorsal fin, a character that has been used to discriminate genera and species within the Helogenidae, has been found to vary within western Amazonian populations of *Helogenes marmoratus*, and such variability is hypothesized to occur in *H. castaneus*. A key to the species and descriptions of recognized taxa are provided.

RESUMEN

Se revisa la familia de bagres neotropicales Helogenidae. Contrariamente a la práctica reciente se reconoce solo un género: *Helogenes* Günther; *Leyvaichthys* propuesto por Dahl se presenta como sinónimo. Se consideran cuatro especies en el género. *Helogenes marmoratus* Günther, tiene amplia distribución a través de la cuenca atlántica de Guianas, el Alto Orinoco de Venezuela y en la cuenca amazónica ha sido colectado en Venezuela, Brasil, Perú y Ecuador. *Helogenes castaneus* (Dahl) se conoce únicamente de los tributarios del Orinoco del este de Colombia. *Helogenes uruyensis* Fernández-Yépez es evidentemente endémico de los alrededores de Auyantepui, Alto Rio Caroni, un tributario sureño del Rio Orinoco en el sureste de Venezuela. *Helogenes gouldingi*, una especie previamente desconocida, es descrita de una serie de especímenes provenientes del sistema del Rio Madeira en Brasil.

Helogenes amazonae Delsman, descrita solamente a partir de un ejemplar colectado cerca de Manaus, Brasil, y *H. unidorsalis* Glodek y Carter, basado en una muestra obtenida en el Rio Bobonaza, en el este del Ecuador, son considerados sinónimos de *H. marmoratus*. La presencia o ausencia de una aleta dorsal adiposa, un carácter que ha sido utilizado para discriminar géneros y especies dentro de Helogenidae, se ha determinado que varía entre poblaciones de *H. marmoratus* de la Amazonia Occidental y tal variabilidad se hipotetiza que también ocurre en *H. castaneus*. Se incluye una clave para las especies, descripciones de los taxa reconocidos, y se discute en amplitud algunos caracteres importantes de la familia.

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The Catfishes of the Neotropical Family Helogenidae (Ostariophysi: Siluroidei)

*Richard P. Vari
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Introduction

The Neotropical catfish family Helogenidae is a distinctive group of small-sized fishes typically inhabiting the smaller blackwater and clearwater streams of the Atlantic drainages of the Guianas, the Río Orinoco tributaries flowing off the Guayana Shield and the piedmont of the Colombian Andes, and a variety of river systems within the Amazon basin. The evidently spotty distribution of the family within this broad geographic expanse is probably more reflective of the secretive nature of the various species than actually representative of the true range of its members. Further collecting activities in appropriate habitats will undoubtedly both fill in gaps within the currently known range of the family and extend those limits farther outwards, most notably in the Orinoco and Amazon basins.

The first member of the family known to science, *Helogenes marmoratus*, was described by Günther (1863:443) from two specimens collected in the Essequibo River system of British Guiana (the present Guyana). Günther expanded the originally very brief account of the species the following year in his catalogue (1864:66). That more comprehensive description was the basis for citations of the species by Eigenmann and Eigenmann (1888:120, 1891:35) and Eigenmann (1910:398), and was paraphrased by Eigenmann and Eigenmann (1890:312) in the description of the species in their monograph on the catfishes of South America. Forty-five years passed between the original report of the species and its second collection by Eigenmann at several localities in British Guiana during his expedition of 1908. Those more extensive series of specimens served as the basis

for the redescription of the species by that author (Eigenmann, 1912:207) and for the first illustration of the fish. In the same publication Eigenmann removed *Helogenes* from the Hypophthalmidae, to which it had been assigned previously, and described a new family, the Helogeneidae (= Helogenidae, see family discussion), consisting of the single contained species *Helogenes marmoratus*. That species has subsequently been reported from localities in Surinam (Steindachner, 1915:86; Boeseman, 1952:182, 1953:9, 1954:20), French Guiana (Mees, 1983:56), Brazil (Steindachner, 1915:86), and Peru (Ortega and Vari, 1986:16).

The Helogenidae remained monotypic for nearly eight decades until Delsman (1941:80) described a second nominal form, *Helogenes amazonae*, based on a single specimen collected in the vicinity of Manaus, Brazil. Dahl (1960:303) increased both the generic and specific taxonomic diversity of the family with his description of *Leyvaichthys castaneus* from the Río Guayabero of southeastern Colombia. *Helogenes* was subsequently further expanded by the description of a subspecies, *H. marmoratus uruyensis* (Fernández-Yépez, 1967:166), from the Río Uruyén of southeastern Venezuela, and by the proposal of a third nominal species, *H. unidorsalis*, from eastern Ecuador by Glodek and Carter (1978:75). The anatomy of the Weberian Apparatus and associated bones of *Helogenes* was described by Chardon (1968:152). Lundberg and Baskin (1969) discussed aspects of its caudal skeleton morphology, and Lundberg (1975) described features of the cranial anatomy of the genus.

Our recent sampling of the ichthyofauna of the Río Madre de Dios drainage system of southeastern Peru revealed populations of a helogenid species demonstrating unexpected variation in some morphological features. This variability leads us to an appraisal of the utility of some characters in distinguishing nominal genera and species within the Helogenidae. The most notable of the evidently

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plastic characters found in these Peruvian populations involved the size of the adipose fin, which covered the spectrum from relatively small, through very small, to being totally absent. Such variability at the population level was troublesome because the presence or absence of that fin had been used to distinguish, wholly or in part, the genus *Leyaichthys* from *Helogenes* and to delimit *H. unidorsalis* within *Helogenes*. Further examination of other helogenid material from diverse regions of the Neotropics indicated that the resolution of the question of the significance of this variability, and other systematic problems, necessitated a revisionary study of the family based on extensive, more geographically encompassing series of specimens.

METHODS AND MATERIALS.—Counts of anal- and caudal-fin rays were made on specimens and confirmed in many cases by examination of radiographs. The two, or more rarely three, anterior anal-fin rays are relatively small and are not always readily apparent in external examination, particularly in more recently collected specimens with darkly pigmented anal fins. Damaged and regenerated caudal-fin rays in some rare instances present externally spurious fin ray counts, which can be resolved via examination of radiographs. The vertebral count is the number of free vertebrae posterior to the anterior vertebral (Weberian) complex and includes the fused PU_1+U_1 complex as a single element. That count does not include the five vertebrae incorporated into that complex (Chardon, 1968:155; personal observation), which cannot be discriminated in radiographs. The numbers in parentheses that follow a particular count of free vertebrae are the number of radiographed specimens with that count. In the "Key" and species accounts, subunits of the head are presented as proportions of head length (HL). Head length itself and measurements of medial mandibular barbel length and of body parts are given as proportions of standard length (SL). In the species descriptions the value of the holotype or lectotype for a count, when available, is given in brackets.

The "Material Examined" section of each species account is arranged in the following sequence: total number of specimens of the species examined (in parentheses the number of specimens forming the basis for the presented meristic and morphometric data, and the range of standard lengths (in mm) for these specimens), collection locality of the specimens, institutional abbreviation, register numbers, number of specimens in the lot (in parentheses the number of specimens in the lot from which counts and measurements were taken, if less than the total number of specimens, and the standard lengths (in mm) of those individuals). In some instances anal-fin ray counts were taken from specimens that were not used for other counts and measurements.

The various helogenid species demonstrate a high degree of morphological uniformity in numerous characters. In order to reduce repetition in the species accounts, such

invariant characters are described in the family diagnosis, but typically are not repeated in the subsequent species descriptions.

ABBREVIATIONS.—The following abbreviations for institutions and collections are used.

AFY	Augustín Fernández-Yépez, personal collection (material later transferred to MAC, then to MBUCV)
AMNH	American Museum of Natural History, New York
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
FMNH	Field Museum of Natural History, Chicago
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels
MAC	Ministerio de Agricultura y Cria, Caracas (collections now at MBUCV)
MBUCV	Museo de Biología, Instituto de Zoología Tropical, Universidad Central de Venezuela, Caracas
MZUSP	Museu de Zoologia da Universidade de Sao Paulo
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C.
NMW	Naturhistorisches Museum, Vienna
UF	University of Florida, Florida State Museum, Gainesville
USM	Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima
USNM	former United States National Museum collections deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA	Zoologisch Museum, Amsterdam

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Family HELOGENIDAE

DIAGNOSIS.—Small-sized fishes; largest individual examined 73.0 mm SL. Body naked, trunk and tail laterally compressed, without bony plates; middorsal groove often extending between posterior end of head and origin of rayed dorsal fin. Dorsal fin length short, base constricted, origin of fin located distinctly closer to hypural joint than to tip of snout, with five rays. Dorsal and pectoral fins lacking spines. Pectoral-fin margin rounded, moderately developed; appressed fin reaching to region of vertical line through origin of pelvic fin, with seven rays, lateral fin ray unbranched. Anal fin elongate, margin straight or slightly convex anteriorly, rounded posteriorly, base fleshy. Anal-fin rays 32 to 49. Anterior two or three anal-fin rays small, often enveloped by anteriorly fleshy basal portion of fin; first and sometimes second ray not associated with a proximal pterygiophore. Anterior 15 or more anal-fin rays unbranched. Origin of anal fin proximate to rear portion of pelvic fins, distinctly anterior of vertical through origin of dorsal fin. Pelvic fin relatively short, margin rounded, with six rays, lateral fin-ray unbranched; posterior portion of appressed fin reaching beyond origin of anal fin. Adipose dorsal fin present or absent, when present small to minute; with an associated basal cartilaginous element similar in form to a proximal radial. Caudal fin forked, ventral lobe larger and longer than dorsal lobe. Fifteen or 16 principal caudal-fin rays; seven principal rays in dorsal lobe of fin, eight or nine in ventral lobe of fin.

Head relatively wide, profile rounded; with thick, loose, fleshy covering. Eyes small, dorsally located, orbital margin not free. Gill opening extending far forward ventrally, membranes free from isthmus. Six simple barbels, nares without barbels. Maxillary barbel moderately developed, extending posteriorly in a groove under eye. Mandibular barbels moderately developed, medial pair usually longer

than lateral pair, sometimes subequal. Mouth relatively wide. Upper jaw longer than lower, extending posteriorly to beyond vertical through anterior margin of eye, sometimes to vertical through posterior margin of eye. Lips fleshy. Margin of lower jaw crescent-shaped in ventral view. Two rows of teeth on premaxilla in juveniles, inner row lost in adults of some species, teeth of inner row smaller than those of outer, often difficult to locate in fleshy lining of mouth. Lower jaw with a band of cardiform teeth, teeth of outermost row somewhat enlarged. Two separate patches of teeth on vomer; teeth of pharyngeal tooth plates on dorsal and ventral portions of gill arches unicuspidate, conical. Gill rakers very short. Twelve or 13 branchiostegal rays.

Five vertebrae in anterior vertebral (Weberian) complex; free vertebrae posterior to complex 36 to 40; 36 and 40 relatively rare. Hypurals one and two fused, joined to PU₁+U₁; hypurals three and four and U₂ autocentrum fused into a single autogenous complex; hypural five autogenous (Figure 1). Secondary hypurapophysis present on element formed by fused first and second hypurals. One epural.

Overall coloration on head and body brown to dark brown, dark pigmentation of body extending onto basal one-third of caudal fin; dark coloration on caudal fin with a discrete vertical posterior margin.

ECOLOGY.—*Helogenes* species typically inhabit clear or blackwater streams either in rain or gallery forests.

REMARKS.—Günther, in his original description of *Helogenes* (1863:443), did not assign the genus to a taxon of higher rank. The following year in his "Catalogue of Fishes" (1864:66) he placed *Helogenes* in his group Hypophthalmina along with the Neotropical freshwater genus *Hypophthalmus*. The association of those two genera was continued by Eigenmann and Eigenmann (1888:120, 1890:312, 1891:35) and Eigenmann (1910:398), who recognized a family Hypophthalmidae that consisted of *Helogenes* and *Hypophthalmus*. In 1912 Eigenmann (p. 207) removed *Helogenes marmoratus*, the then only known species in the genus, to its own family, the Helogeneidae (= Helogenidae). In his key to the catfishes of British Guiana (1912:119) he noted a series of differences between the Helogenidae and the Hypophthalmidae (*sensu stricto*) but did not elaborate on these characters in the text. Although he commented later in the same work (p. 207) on the similarities between the two families, particularly the relatively long anal fin and posterior position of the rayed dorsal fin, he nonetheless concluded that *Helogenes* "differed from it [*Hypophthalmus*] in so many other essential characters that it is but remotely related to that genus." Eigenmann did not hypothesize an alternative phylogenetic relationship for the Helogenidae.

A discrete family Helogenidae was subsequently recognized by Regan (1911:573), Jordan (1923:150), Berg (1940:449), Gosline (1945:53), and Greenwood et al.

(1966:396). Bertin and Arambourg (1958:2306), in a significant systematic realignment, placed *Helogenes* in their broadly defined Schilbeidae that also included the Old World Pangasiidae and Schilbeidae together with the Neotropical Hypophthalmidae. In his description of *Leyvaichthys castaneus*, a new genus and species of helogenids, Dahl (1960:304) suggested that the Helogenidae might be "phylogenetically allied" to the Neotropical family Cetopsidae. Chardon (1968:152) described the anatomy of the Weberian Apparatus and associated systems in *Helogenes*, and noted similarities of that genus with the catfishes of the Old World families Siluridae and Schilbeidae and the Neotropical families Diplomystidae and Trichomycteridae. In the classification summarizing his conclusions, that author (1968:225) created the superfamily Helogeneoidea for *Helogenes* and allied that taxon with the Old World superfamilies Siluroidea and Amblycipitoidea. The three superfamilies together constituted his Siluroidei. Lundberg and Baskin (1969:14, 17, 41) discussed the caudal-fin osteology of *Helogenes marmoratus*, but were unable to make a definitive statement about the phylogenetic relationships of the species based on information from that body system. Most recently Géry (1984:358) suggested that the family is primitive, but did not place that statement in an explicit phylogenetic context. In light of the divergent alternative hypotheses on the relationships of the family that have been advanced by different authors, and in the absence of a phylogenetic hypothesis based on derived characters from multiple body systems, we prefer to retain a separate Helogenidae within the Siluroidei (sensu Fink and Fink, 1981) without formally aligning the family with a more inclusive taxon within that order.

Eigenmann (1912) in his original description of the family used the name Helogeneidae, a practice followed by most of the authors who published on the group during the following seven decades. Steyskal (1980:174) pointed out that Helogeneidae was an incorrect derivation of a family name based on *Helogenes*, because "Names ending in *-es* drop that syllable for their stems" in forming the family name. As such the stem derived from *Helogenes* is "Helo-gen," and the correct spelling of the family name is Helogenidae.

THE ADIPOSE DORSAL FIN IN THE HELOGENIDAE

In his original description of *Leyvaichthys*, Dahl (1960:302) distinguished that genus from *Helogenes* partially on the basis of the lack of the small adipose dorsal fin, the possession of which was considered characteristic of the latter genus. More recently Glodek and Carter (1978:77) in their description of *Helogenes unidorsalis* distinguished their species from other nominal taxa in the genus partly due to the absence of an adipose fin.

The presence and degree of development of the adipose

dorsal fin is variable in the series of specimens of *Helogenes marmoratus* we collected in the Río Madre de Dios basin of southeastern Peru (USNM 264030; USM 1595; USM 1596). Those 28 specimens collected in a small brook draining into the Río Tambopata show a gradient in adipose-fin size. Twelve individuals have relatively small adipose fins, nine specimens have very small, reduced adipose fins, three examples have greatly reduced, vestigial fins, and adipose fins were completely lacking in the remaining four specimens. These four classes of specimens are otherwise inseparable meristically and morphometrically (Table 1). This continuum in adipose-fin size indicates that the presence or absence of the fin is intraspecifically variable at least within some populations of *Helogenes marmoratus*. In the Helogenidae such within-species variability in the relative size of the adipose fin also occurs in populations of *H. castaneus* and it is further hypothesized that the fin is absent in some members of that species (see "Remarks" under *H. castaneus*).

Comparable intraspecific variability in the presence of a small adipose dorsal fin occurs in the auchenipterid catfish *Auchenipterus nuchalis* (Spix), which typically has an adipose fin. *Ceratocheilus osteomystax* described by Miranda Ribeiro (1918:644), and placed into the synonymy of *Auchenipterus nuchalis* by Mees (1974:22), was originally delimited in part by its lack of an adipose fin, a character that has on further analysis proved to be intraspecifically variable. Intraspecific variability in the presence or absence of an adipose fin among other ostariophysans has also been reported within the Characiformes for the lebiasinids *Nannostomus eques* Steindachner (1876:126), *N. harrisoni* Eigenmann (Weitzman, 1966:6, 39), and the characid *Klausewitzia aphanes* Weitzman and Kanazawa (1977:155). Such intraspecific variability was also the basis for the description of the invalid curimatid genus *Curimatoides* by Fowler (1940:255) (personal observation, R.P.V.).

The variability in the presence and size of the adipose dorsal fin within populations of *Helogenes marmoratus*, *H. castaneus*, and other Neotropical siluroids and characiforms indicates that the presence or absence of the fin, particularly when the fin is typically relatively small, is of questionable utility in independently delimiting taxa at the specific and supraspecific levels.

The variability in the presence or absence of the adipose fin within *Helogenes* is apparently limited to populations along the western rims of the Amazon and Orinoco drainage basins. Whereas *Helogenes marmoratus* typically has an adipose fin, that structure is not developed in some individuals from southeastern Peru (material cited above) and eastern Ecuador (type series of *H. unidorsalis*, = *H. marmoratus*). *Helogenes castaneus* from eastern Colombia is hypothesized to demonstrate comparable variability in the development of the structure (see "Remarks" under that species). This geographic pattern may, however, be primarily a consequence of the relatively more intensive, though by no

TABLE 1.—Morphometrics and anal-fin ray count variation in specimens of *Helogenes marmoratus* with different degrees of development of the adipose dorsal fin (number of specimens in parentheses). All material from same stream in the Río Madre de Dios system of southeastern Peru (USNM 264030, 19 specimens; USM 1595, 4 specimens; USM 1596, 5 specimens). (Standard length is expressed in mm; measurements 1 to 11 are proportions of standard length, 12 to 16 are proportions of head length.)

	Small (12)	Reduced (9)	Vestigial (3)	Absent (4)
Standard length	31.0–62.5	50.9–65.3	39.1–47.9	42.2–63.0
1. Snout to origin of dorsal fin	0.63–0.68	0.64–0.69	0.66–0.67	0.63–0.66
2. Snout to origin of pelvic fin	0.33–0.37	0.33–0.37	0.35–0.37	0.36–0.37
3. Snout to origin of anal fin	0.38–0.48	0.43–0.45	0.43–0.45	0.39–0.44
4. Length of base of anal fin	0.50–0.57	0.54–0.58	0.54–0.57	0.55–0.56
5. Distance between rayed and adipose dorsal fins	0.09–0.13	0.10–0.13	0.10–0.11	–
6. Greatest body depth	0.17–0.23	0.19–0.24	0.17–0.21	0.20–0.23
7. Depth of caudal peduncle	0.10–0.13	0.12–0.15	0.11–0.13	0.11–0.12
8. Length of medial mandibular barbel	0.27–0.38	0.28–0.33	0.29–0.34	0.23–0.32
9. Length of pectoral fin	0.20–0.24	0.21–0.23	0.21–0.22	0.19–0.24
10. Length of pelvic fin	0.09–0.13	0.10–0.13	0.10–0.12	0.11–0.13
11. Head length	0.20–0.22	0.18–0.22	0.20–0.21	0.17–0.21
12. Interorbital width	0.43–0.52	0.46–0.53	0.48–0.51	0.46–0.49
13. Snout length	0.34–0.50	0.31–0.45	0.35–0.42	0.33–0.39
14. Orbital width	0.09–0.13	0.08–0.12	0.09–0.13	0.09–0.12
15. Length of postorbital portion of head	0.46–0.63	0.49–0.59	0.54–0.57	0.51–0.58
16. Gape width	0.48–0.62	0.54–0.68	0.57–0.59	0.52–0.60
Anal-fin rays	43–48	43–46	43–45	43–46

means satisfactory, collecting efforts that have taken place in the western portions of Amazonia and the Orinoco basin than reflective of the true geographic limits of such morphological variability.

THE CAUDAL SKELETON IN THE HELOGENIDAE

Lundberg and Baskin (1969), in their analysis of the caudal fin skeleton of various groups of catfishes, were limited in their comparative studies of the Helogenidae in having access only to specimens of *Helogenes marmoratus* and by the availability of only a single cleared and stained individual of the species. Examination of a more extensive series of cleared and stained specimens has revealed additional variability in one of the characters they discuss, and indicates that the specimen they reported on was evidently abnormal in the form of the element they termed the U_2 autocentrum.

Lundberg and Baskin (1969:35, table 2) cite the Helogenidae as being characterized by the possession of 16 principal caudal-fin rays, with seven rays in the upper lobe and nine in the lower lobe of the fin. Our examination of more extensive series of specimens has confirmed that count for *Helogenes marmoratus* Günther and *H. uruyensis* Fernández-Yépez. The two other recognized species, *H. castaneus* (Dahl) and *H. gouldingi* described in this paper, have the number of principal caudal-fin rays reduced to 15, with

only eight principal rays present in the lower lobe of the fin. If a decreased number of caudal-fin rays is indeed derived (Lundberg and Baskin, 1969:34), then the presence of only eight rays in the lower lobe of the caudal fin can be hypothesized to be an advanced condition indicating that *H. castaneus* and *H. gouldingi* are sister species.

Lundberg and Baskin (1969:17, table 1, fig. 7a) also note that *Helogenes* is unique among the catfishes they examined in having an autogenous U_2 autocentrum, which is separate from both the fused PU_1+U_1 and the single compound upper hypural element (hypurals three and four). Examination of 12 cleared and stained specimens of *H. marmoratus* from Guyana, Venezuela, and Peru, and an individual of *H. gouldingi*, along with reference to radiographs of over 100 other specimens of all nominal forms has shown that although the U_2 autocentrum of helogenids is free from the PU_1+U_1 compound centrum, it is, nonetheless, fused to the compound upper hypural element derived from the third and fourth hypurals (Figure 1). The specimen reported on by Lundberg and Baskin was presumably aberrant in having a totally autogenous U_2 autocentrum. The form of the U_2 autocentrum and neighboring ossifications in helogenids rather than being unique among catfishes is instead comparable to the association of those elements reported by those authors (1969:7, table 1) for most of the Neotropical family Aspredinidae and some members of the Old World families Amblycipitidae and Mochokidae.

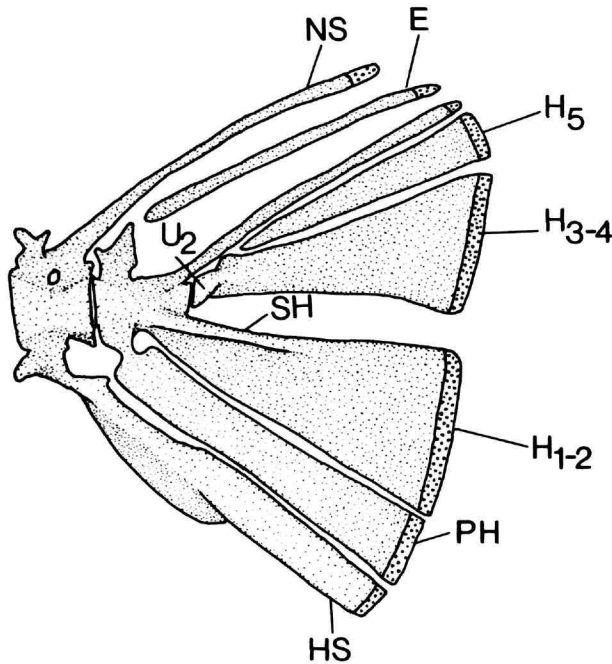


FIGURE 1.—*Helogenes marmoratus*, USM 1595, caudal skeleton (E = epural, H = hypurals (1 to 5), HS = hemal spine, NS = neural spine, PH = parhypural, SH = secondary hypurapophysis, U₂ = second ural centrum).

Genus *Helogenes* Günther

Helogenes Günther, 1863:443 [type-species: *Helogenes marmoratus* Günther, 1863, by monotypy].

Leyvaichthys Dahl, 1960:302 [type-species: *Leyvaichthys castaneus* Dahl, 1960 (= *Helogenes castaneus*), by original designation; new synonymy].

Leyvaichthys.—Glodek and Carter, 1978:76 [misspelling of *Leyvaichthys*].

DIAGNOSIS.—As for the family.

REMARKS.—Dahl (1960:304) in his original description of *Leyvaichthys* distinguished his genus from *Helogenes* because "There is no vestige whatsoever of an adipose fin . . . the position far back of the dorsal fin, the very large number of anal rays and the peculiar dentition." As discussed above (see "The Adipose Dorsal Fin in the *Helogenidae*"), the presence of an adipose fin and its size, when present, are variable at least within western Amazonian populations of *Helogenes marmoratus*. The size of the fin is relatively variable in some populations of *H. castaneus* from Colombia, and it would appear that there is intraspecific variability in the presence of the adipose fin in that species (see "Remarks" under *H. castaneus*). The absence of the fin is consequently not considered to be an appropriate basis for delimiting a second genus within the family.

In his table detailing the morphometric values of the holotype of *Leyvaichthys castaneus*, Dahl (1960) indicates that the distance from the snout to the origin of the rayed dorsal fin in that specimen is 0.665 of "skeletal length" (presum-

ably standard length). That value agrees well with the range for that measurement in the material identified as *Helogenes castaneus* in this study (0.65–0.71 of SL), but more significantly relative to the question of the recognizability of *Leyvaichthys*, that value is overlapped by the ranges for that measurement found in examined specimens of *Helogenes marmoratus* (0.52–0.71 of SL) from diverse portions of the geographic distribution of that species. As such, that morphometric character is not useful in delimiting those nominal species, let alone the two genera. The number of anal-fin rays cited by Dahl (45 to 49) differed significantly from the 37 to 40 listed by Eigenmann (1912:208) for Essequibo River *H. marmoratus*, but overlapped the 41 to 46 anal-fin rays cited for the species by Steindachner (1915:87), and is within the range of anal-fin rays of *H. marmoratus* found in this study (39 to 48). Thus anal-fin ray numbers also fail to delimit *Leyvaichthys* from *Helogenes*.

Dahl characterized *Leyvaichthys* as having a single row of teeth on the premaxilla, whereas *Helogenes marmoratus* has two rows of teeth on that element. The specimens identified as *Helogenes castaneus* in this study demonstrate what appears to be ontogenetic variability in the number of tooth rows on the premaxilla. Specimens of approximately 36 to 42 mm SL have a complete outer row of dentition and a less well-developed inner row of smaller teeth often limited to the lateral margins of the jaw. The inner tooth row is lacking in the 40 to 47 mm SL specimens of the species examined. Because the type series reported on by Dahl consisted of individuals of over 47 mm SL, the observed lack of the inner premaxillary teeth in those specimens can be assumed to have been a consequence of a similar process of ontogenetic loss.

Dahl described the outer row of teeth in each jaw of *Leyvaichthys* as having serrated edges. Such a modification of the smooth conical teeth typical for most catfishes has not been found in the specimens herein equated with *Helogenes castaneus*, nor are they present in any other member of the family. In the absence of the type series of *Leyvaichthys castaneus* on which we could confirm this character, and given the evident lack of such dentition in catfishes, along with the absence of tooth serrations in Colombian helogenid material that otherwise fits the description of *Leyvaichthys castaneus*, we assume that the reported presence of tooth serrations on the outer tooth rows in that species represents an erroneous observation.

The characters listed by Dahl as separating *Leyvaichthys* from *Helogenes* either fail to distinguish even the single contained nominal species at the specific level (absence of adipose fin, relative length from snout tip to origin of rayed dorsal fin, anal-fin ray count), delimit only the largest adults (number of premaxillary tooth rows) or, in the case of the reported tooth serrations, are considered to represent, in the light of available information, an erroneous observation. Only the absence of an inner tooth row on the premaxilla

of larger specimens distinguishes *Helogenes castaneus* from the three other species in the family. We prefer not to formalize this minor dentitional difference at the generic level, given our current uncertainty as to the relationships of the various helogenid species. Furthermore, the recognition of *Leyvaichthys* for the species herein termed *Helogenes castaneus* would mean that the genus *Helogenes*, thus restricted to the three other species in the family, would be defined by the retention of an inner row of premaxillary teeth in the adults, a primitive character. Such a primitive character is not an appropriate basis for advancing a hypothesis that the genus *Helogenes*, in such a restricted sense, would constitute a natural assemblage. Indeed the only

character uncovered possibly pertinent to the question of intrafamilial relationships, the reduced number of principal rays in the lower lobe of the caudal fin (see "The Caudal Skeleton in the Helogenidae"), suggests that *Helogenes castaneus* is more closely related to *H. gouldingi* than the latter species is to the remaining members of the family. If that hypothesis of relationships is correct, the separation of *H. castaneus* in *Leyvaichthys* and the alignment of *H. gouldingi* with *H. marmoratus* and *H. uruyensis* in *Helogenes* would result in the latter genus being non-monophyletic, because it would not consist of all descendants of the hypothesized common ancestor. For these reasons *Leyvaichthys* Dahl is herein placed into the synonymy of *Helogenes* Günther.

Key to the Species of *Helogenes* Günther

1. 15 principal caudal fin rays; with eight principal rays on lower lobe of caudal fin 2
 16 principal caudal fin rays; with nine principal rays on lower lobe of caudal fin 3
2. 39 to 43 anal rays. Distance from tip of snout to origin of rayed dorsal fin 0.57–0.60 of SL. Snout length 0.36–0.40 of HL. Distance between rayed dorsal fin and adipose dorsal fin 0.16–0.19 of SL *H. gouldingi*, new species
 43 to 49 anal rays. Distance from tip of snout to origin of rayed dorsal fin 0.65–0.71 of SL. Snout length 0.27–0.36 of HL. Distance between rayed dorsal fin and adipose dorsal fin 0.11–0.15 of SL *H. castaneus* (Dahl), new combination
3. 32 to 37 anal-fin rays *H. uruyensis* Fernández-Yépez, new status
 39 to 48 anal-fin rays *H. marmoratus* Günther

***Helogenes gouldingi*, new species**

FIGURES 2–4

DIAGNOSIS.—The possession of 15 principal caudal-fin rays, with eight principal rays in the lower lobe of the fin, distinguishes *Helogenes gouldingi* from both *H. uruyensis* and *H. marmoratus*, which have 16 principal caudal-fin rays, with nine principal rays in the lower lobe of the fin. The 39 to 43 anal-fin rays of *Helogenes gouldingi* further separate it from *H. uruyensis*, which has 32 to 37 rays. *Helogenes gouldingi* and *H. castaneus* are separable in the number of anal-fin rays (39 to 43 versus 43 to 49), relative snout lengths, and relative distance between the rayed and adipose dorsal fins. Differences in the relative distances from the snout to the origin of the pelvic fin, and snout to the origin of the anal fin, and relative lengths of the base of the anal fin, and medial mandibular barbel further distinguish *H. gouldingi* from *H. uruyensis* (see "Key," Figure 2, and Table 2).

DESCRIPTION.—Morphometrics of the holotype and paratypes are given in Table 2.

Dorsal profile of body smooth, slightly convex from snout to dorsal margin of caudal peduncle. Ventral profile of body gently curved from lower jaw to pelvic-fin origin. Base

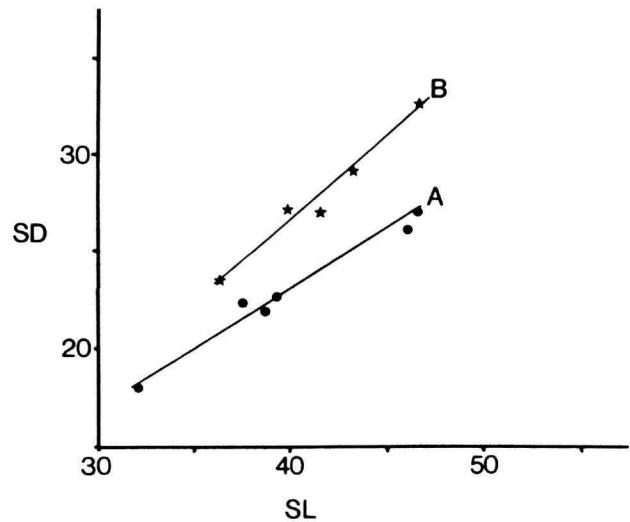


FIGURE 2.—Graph of distance from tip of snout to origin of rayed dorsal fin (SD) against standard length (SL) for *Helogenes gouldingi*, new species (A), and *Helogenes castaneus* (B) (both in millimeters, with regression lines for each species; $r_2=0.97$, regression lines significantly different [$P=0.05$]).

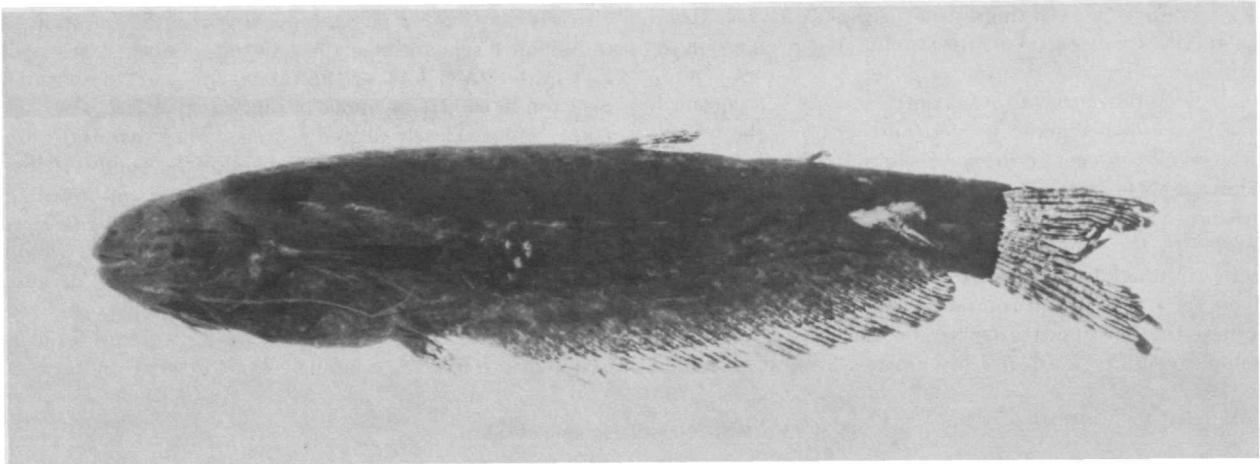


FIGURE 3.—*Helogenes gouldingi*, new species, holotype, MZUSP 28854, 46.5 mm SL; Rio Madiera, Amazonas, Brazil.

TABLE 2.—Morphometrics of the species of *Helogenes*. (Standard length is expressed in mm; measurements 1 to 11 are proportions of standard length; 12 to 16 are proportions of head length. See "Material Examined" for each species for information on measured specimens.)

	<i>castaneus</i>		<i>uruyensis</i> Paratypes		<i>marmoratus</i>			<i>gouldingi</i>		
	Range	\bar{x}	Range	\bar{x}	Lectotype	Non-types		Holotype	Paratypes	
						Range	\bar{x}		Range	\bar{x}
Standard length	23.2–46.6		36.5–43.1		56.8	19.7–73.0		46.5	27.0–46.0	
1. Snout to origin of dorsal fin	0.65–0.71	0.685	0.54–0.57	0.559	0.62	0.52–0.71	0.644	0.58	0.57–0.60	0.576
2. Snout to origin of pelvic fin	0.32–0.34	0.327	0.37–0.40	0.375	0.36	0.31–0.42	0.355	0.32	0.30–0.33	0.318
3. Snout to origin of anal fin	0.40–0.42	0.413	0.46–0.51	0.482	0.43	0.37–0.50	0.438	0.44	0.42–0.44	0.433
4. Length of base of anal fin	0.57–0.63	0.592	0.47–0.52	0.491	0.58	0.49–0.61	0.547	0.57	0.54–0.57	0.552
5. Distance between dorsal and adipose dorsal fins	0.11–0.15	0.124	0.16–0.19	0.174	0.20	0.09–0.21	0.134	0.18	0.16–0.19	0.178
6. Greatest body depth	0.20–0.23	0.212	0.18–0.22	0.193	0.23	0.16–0.26	0.206	0.22	0.15–0.20	0.182
7. Depth of caudal peduncle	0.11–0.13	0.123	0.12–0.14	0.128	0.12	0.09–0.15	0.120	0.11	0.10–0.13	0.118
8. Length of medial mandibular barbel	0.27–0.40	0.339	0.19–0.25	0.223	0.36	0.16–0.47	0.310	0.40	0.38–0.43	0.407
9. Length of pectoral fin	0.20–0.22	0.209	0.18–0.20	0.186	0.21	0.16–0.23	0.202	0.20	0.20–0.22	0.204
10. Length of pelvic fin	0.08–0.11	0.097	0.09–0.11	0.105	0.12	0.08–0.13	0.111	0.12	0.10–0.12	0.112
11. Head length	0.18–0.21	0.191	0.20–0.22	0.213	0.21	0.17–0.24	0.205	0.21	0.20–0.22	0.210
12. Interorbital width	0.39–0.51	0.467	0.50–0.58	0.542	0.47	0.41–0.56	0.486	0.44	0.46–0.50	0.468
13. Snout length	0.27–0.36	0.335	0.39–0.46	0.423	0.41	0.31–0.45	0.356	0.36	0.36–0.40	0.382
14. Orbital width	0.10–0.15	0.118	0.09–0.13	0.113	0.11	0.07–0.14	0.112	0.12	0.10–0.14	0.123
15. Length of postorbital portion of head	0.51–0.56	0.544	0.48–0.55	0.510	0.48	0.43–0.63	0.537	0.56	0.54–0.63	0.556
16. Gape width	0.45–0.57	0.497	0.52–0.60	0.571	0.53	0.44–0.67	0.552	0.47	0.53–0.58	0.561

of anal fin slightly convex anteriorly, straight posteriorly. Pectoral fin with seven rays, reaching posteriorly to vertical through insertion of fourth to sixth anal-fin ray. Anal-fin margin straight anteriorly, rounded posteriorly. Anal-fin rays 39 to 43 [43]. Caudal fin with 15 principal rays; eight principal rays in lower lobe. Dorsal fin small, with five rays. Small adipose fin present in all examined specimens.

Two rows of teeth on premaxilla, inner series smaller, less evident. Lower jaw with a band of cardiform teeth, outer row distinctly larger.

Anterior and posterior nares well separated, anterior nares slightly tubular. Maxillary barbel extending posteriorly to beyond end of pectoral fin. Medial mandibular barbel extending to or slightly beyond middle of pectoral fin. Lateral mandibular barbel distinctly shorter than medial.

Five vertebrae in anterior vertebral complex; free vertebrae posterior to complex 38 (6) [38].

COLORATION.—Overall coloration dark brown, mottled; head distinctly darker dorsally. Dark body pigmentation

TABLE 3.—Frequency distribution of numbers of anal-fin rays in *Helogenes uruyensis*, *H. castaneus*, *H. gouldingi*, and major geographic subunits of *H. marmoratus*.

Species	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	N	\bar{x}
<i>H. gouldingi</i>								1	2	1	1	2							7	41.14
<i>H. castaneus</i>												1	5	12	7	8	5	4	42	46.12
<i>H. uruyensis</i>	1	1	1	1	1	4													9	36.14
<i>H. marmoratus</i>																				
Guyana								2	5	6	8	3	1						25	41.32
Surinam									1	4	8	10	10	4	2	1			40	43.22
Venezuela										1	10	10	5	5	3	—	1		35	43.48
Brazil											1	1	2	4	1	1	1		11	44.91
Ecuador														3	—	—	2		5	45.20
Peru												8	9	6	5	2	1		31	44.58

FIGURE 4.—Geographic distribution of *Helogenes gouldingi* (star), *Helogenes castaneus* (circle with enclosed star indicates type-locality, solid circle indicates localities of other examined specimens), and *Helogenes uruyensis* (triangle) (some symbols represent more than one collecting locality or lot of specimens).

extending onto basal one-third of caudal fin, posterior margin of pigmentation band very distinct, with a straight or slightly wavy border. Rayed dorsal fin mottled, darker at base. Caudal fin dark basally, mottled over posterior two-thirds. Anal fin dark brown at base, mottled distally, more so along posterior portion. Pectoral and pelvic fins ranging from mottled, particularly basally, to dark brown.

DISTRIBUTION.—Known only from the type-locality (Figure 4).

ECOLOGY.—The type series was collected in a small black-water tributary of the Rio Madeira.

ETYMOLOGY.—Named for Michael Goulding, the collector of the type series, in recognition of his contributions to increasing our knowledge of the Amazonian fish fauna.

MATERIAL EXAMINED.—8 specimens (7, 27.0–46.5).

Holotype: BRAZIL. Amazonas: Igarapé 15 km from Humaitá along the Rio Madeira, (7°31'S, 63°02'W), collected by Michael Goulding, 7 Aug 1984, MZUSP 28854, 1 (46.5).

Paratypes: 7 specimens, taken with holotype: MZUSP 28855, 3 (27.0–37.4); USNM 269446, 4 (25.8–46.0; one specimen cleared and counterstained for cartilage and bone).

Helogenes castaneus (Dahl), new combination

FIGURES 2, 4, 5

Leyvaichthys castaneus Dahl, 1960:303 [type-locality: Colombia: Rio Guayabero].—Cala 1977:11 [Colombia: Rio Guayabero system].

Leyvaichthys castaneus.—Glodek and Carter, 1978:80 [distribution; generic name misspelled].

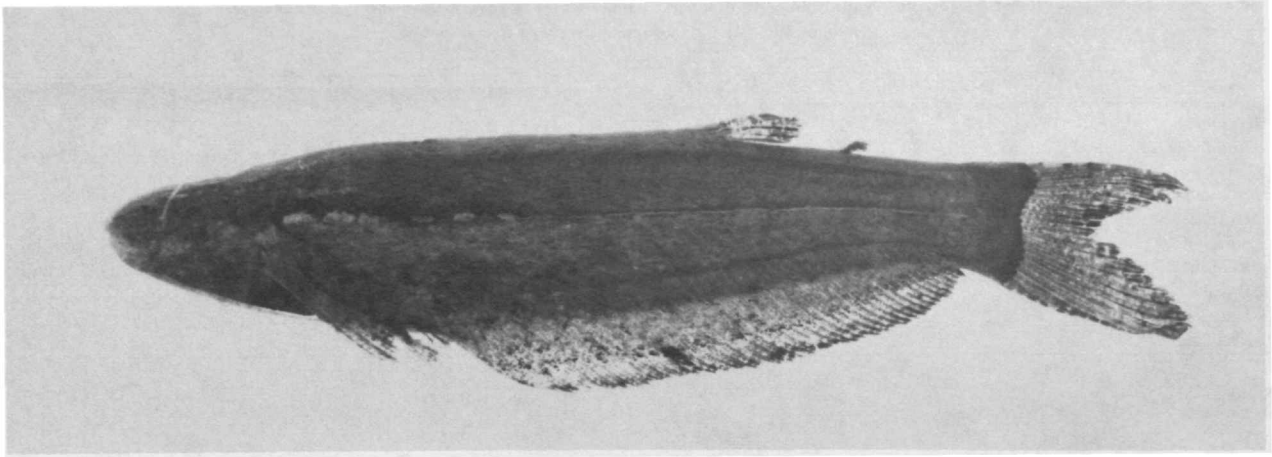


FIGURE 5.—*Helogenes castaneus*, ANSP 128703, 46.6 mm SL; Río Meta system, Colombia.

DIAGNOSIS.—*Helogenes castaneus* is readily distinguishable from *H. uruyensis* in the number of anal-fin rays (43 to 49 in contrast to 32 to 37) and a number of morphometric differences (Table 2). The presence of eight principal rays in the lower lobe of the caudal fin of *H. castaneus* separates it from *H. marmoratus*, which has nine principal rays in the lower lobe of that fin. The 43 to 49 anal-fin rays of *Helogenes castaneus* discriminate that species from *H. gouldingi*, which has 39 to 43 anal-fin rays. Those two species are also separable in various morphometric characters, most notably their relative snout lengths and in the distance between the rayed and adipose dorsal fins (see "Key" and Figure 2).

DESCRIPTION.—Morphometrics of the examined specimens are given in Table 2.

Dorsal profile of body smooth, slightly convex from snout to dorsal portion of caudal peduncle. Ventral profile of body smooth, convex from lower jaw to origin of pelvic fins. Base of anal fin straight to slightly sigmoid. Pectoral fin with seven rays, extending posteriorly to beyond anus, to or beyond vertical through origin of anal fin. Pelvic fin with six rays, reaching to vertical through insertion of third anal-fin ray. Anal-fin margin straight or slightly convex anteriorly, concave posteriorly. Anal-fin rays 43 to 49 [holotype reported by Dahl as having 49 rays]. Rayed dorsal fin small, with five rays. Adipose dorsal fin present in examined specimens [reported as absent in holotype, not seen by us], of variable size in some population samples. Caudal fin with 15 principal rays; eight principal rays on lower lobe.

Premaxilla with two series of teeth in juveniles, outer row larger; inner row lacking in specimens larger than approximately 47 mm SL. Lower jaw with a band of cardiform teeth, outer series enlarged.

Anterior and posterior nares well separated, both somewhat tubular. Maxillary barbel extending posteriorly somewhat beyond vertical through insertion of pectoral fin.

Medial mandibular barbel extending posteriorly to vertical through origin of anal fin. Lateral mandibular barbel shorter, reaching approximately to vertical through middle of pectoral fin.

Five vertebrae in anterior vertebral complex; vertebrae posterior to complex 36 (4), 37 (9), 38 (5), 39 (1).

COLORATION.—Overall coloration of head and body brown, somewhat mottled, dark body pigmentation extending onto basal one-third of caudal fin; a darker horizontal band extending from rear of head, along and above lateral line for approximately one-third of body length. A series of very lightly pigmented spots located along lateral stripe; spots larger anteriorly, reduced to narrow lines posteriorly. Rayed dorsal fin mottled, darker basally. Adipose fin mottled. Caudal fin with basal one-third dark brown, region of dark pigmentation with a discrete posterior border; margin straight or somewhat wavy. Anal fin mottled. Pectoral and pelvic fins mottled, darker basally.

DISTRIBUTION.—Río Guaviare and Río Meta drainages of the upper Río Orinoco in eastern Colombia (Figure 4).

REMARKS.—Dahl's description of *Leyuichthys castaneus* (1960:303) was based on three specimens collected in the region of the southern Serranía de la Macarena of Colombia in the upper Río Guayabero, a tributary of the Río Guaviare, which is an affluent of the Río Orinoco. We have been unable to locate the type series of the species in any repository, and Dr. P. Cala, who has also attempted to determine the depositories of all of the types of the species described by Dahl, has been similarly unsuccessful (P. Cala, personal communication). We thus assume that the specimens are lost.

The available material of the family Helogenidae from Colombia was all collected in the basin of the Río Meta, the major drainage basin immediately to the north of the Río Guaviare. These Colombian specimens differ from the de-

scription of *Leyvaichthys castaneus* in several details. The differences are, however, either intraspecifically variable in other helogenid species, and their utility in delimiting species within the Helogenidae thus questionable, or in the case of a dentitional character are based on an apparently erroneous observation by Dahl.

Dahl stated that the anal-fin ray count and relative distance from the tip of the snout to the dorsal-fin origin separated *Leyvaichthys* from *Helogenes*. A re-examination reveals that those characters fail to distinguish *Helogenes castaneus* from other species of helogenids (see "Remarks" under discussion of *Helogenes*) and thus are not useful in defining *Leyvaichthys* relative to *Helogenes*. The three most significant of the characters purportedly diagnostic for *Leyvaichthys*, or that require discussion, are the presence or absence of the adipose dorsal fin, the number of branched rays on the caudal fin, and the number of rows of teeth and the form of dentition on the premaxilla.

Although Dahl (1960:302) states that *Leyvaichthys castaneus* "differs in so many characters from *Helogenes* Guenther, that it has been considered necessary to describe it as the type of a new genus . . .," the only character that he specifically cited in the diagnosis of the new genus as differing from the condition in the previously known *Helogenes* was the lack of an adipose dorsal fin. The available specimens of *H. castaneus* demonstrate noticeable variability in the relative size of the adipose dorsal fin. Furthermore, as discussed above (see "The Adipose Dorsal Fin in the Helogenidae") the presence or absence of an adipose fin is intraspecifically variable among helogenids and of is questionable validity as the basis for discriminating taxa at the specific, let alone generic levels, particularly in the absence of other correlated differences. In light of the variability in the presence of the adipose fin in *Helogenes marmoratus*, and given the range in the relative size of that structure in examined Colombian helogenids, we assume that the absence of the adipose fin in the type series of *Leyvaichthys castaneus* represents intraspecific variation.

Dahl (1960:304) described *Leyvaichthys* as having "10 branched rays in the upper and 12 in the lower lobe" of the caudal fin. Such a high branched caudal fin count is unknown in any catfish (see Lundberg and Baskin, 1969:35, for a summary) and differs significantly from the six rays in the upper lobe of the fin and seven or eight in the lower lobe found in examined material of the Helogenidae. Although the specimens herein identified as *Helogenes castaneus* have six branched rays in the upper and seven branched rays in the lower lobe of the caudal fin, they also have four externally visible unbranched rays in the upper lobe of the fin and five in the lower lobe of the fin. The addition of the unbranched rays to the branched ray count would bring the total number of caudal rays, branched and unbranched, to the 10 plus 12 count cited by Dahl. Given the unlikely nature of the number of branched rays cited

by Dahl and the equivalence between the count of total externally visible caudal rays and the figures he presented, Dahl obviously included the externally visible unbranched rays in his count of branched caudal-fin rays.

Dahl (1960:303) stated that *Leyvaichthys castaneus* was characterized by a single row of teeth on the premaxillary. *Helogenes*, in contrast, has two series on that element, although Dahl did not cite that difference. As discussed previously (see "Remarks" under discussion of *Helogenes*), the number of tooth rows in specimens herein considered to be *Helogenes castaneus* are ontogenetically variable, with two rows present in juveniles and only one in adults. Another dentitional character cited by Dahl as characteristic of *Leyvaichthys*, the serrations on the premaxillary teeth, is evidently otherwise unknown in catfishes and has not been encountered in the examined material of the family. As a consequence its cited presence in *Leyvaichthys* is presumed erroneous.

In the absence of the type series of *Leyvaichthys castaneus*, it is not possible to definitely determine whether our supposition about tooth serrations and adipose fin absence is correct. We prefer to identify the Colombian helogenid material we have examined as *Helogenes castaneus*. This decision is based on circumstantial evidence from several systems. If the caudal-fin ray count cited by Dahl does represent the total number of externally visible rays in the caudal fin, then his specimens of *Leyvaichthys castaneus* had eight principal rays in the lower lobe of the caudal fin (seven branched and one unbranched rays). Such a ray count occurs in *H. gouldingi* and the specimens herein considered as *H. castaneus*, but excludes *H. marmoratus* and *H. uruyensis*, which have an additional branched ray in the lower lobe of the caudal fin. The examined Colombian material comes from a region proximate to the type-locality of *Leyvaichthys castaneus*, with both being within the Río Orinoco drainage system. *Helogenes gouldingi*, the second species with eight lower lobe principal caudal rays, in contrast, is known only from the middle Río Madeira system in the Amazon basin. More significantly *Leyvaichthys castaneus* was described by Dahl (1960:309) as having a total of 45 to 49 anal-fin rays, a count in agreement with the 43 to 49 anal-fin rays found in our material, but distinct from the 39 to 43 rays found in *Helogenes gouldingi*. Finally, the larger of the Colombian specimens we have examined are unique among examined helogenids in having only a single series of teeth in the upper jaw, a character noted by Dahl as distinguishing for *Leyvaichthys* (= *Helogenes*) *castaneus*. Thus, the material we identify as *Helogenes castaneus* best fits the original description of the species among examined specimens.

Hopefully further collections can eventually be made in the type-locality to determine whether our assumptions about variability in the presence of the adipose fin and on tooth form are correct. The conservative course of action in which we equate, for the present, the available specimens

from the Colombian portions of the Orinoco basin with *Leyvaichthys* (= *Helogenes*) *castaneus* is preferable to the description of a new and most likely invalid species for these distinctive specimens.

MATERIAL EXAMINED.—47 specimens (25, 23.2–46.6 mm SL).

COLOMBIA. Meta: Caño Angosturas, Hacienda Humacita (03°58.5'N, 73°4.5'W), ANSP 128702, 1 (39.9). Caño Enma, Finca El Viento, 33.5 km NE of Puerto Lopez (04°08'N, 72°39'W), ANSP 128703, 2 (43.3–46.6). Caño El Viento, Finca El Viento (04°08'N, 72°39'W), ANSP 128704, 1 (41.6). Quebrada La Venturosa, between La Balsa and Puerto Lopez (04°05'N, 72°58'W), ANSP 128705, 1 (36.4). Tributary to Río Yucao, approximately 4.7 km W of Puerto Gaitan, UF 33472, 41 (20, 23.2–38.8). Río Yucao, on dirt road paralleling Río Meta, UF 33565, 1.

***Helogenes uruyensis* Fernández-Yépez, new status**

FIGURES 4, 6

Helogenes marmoratus uruyensis Fernández-Yépez, 1967:166, pl. 2, pl. 3: fig. 2, table 2 [type-locality: Venezuela: Guayana, Río Uruyén near Auyantepui].—Mago-Leccia, 1970:82 [citation].—Glodek and Carter, 1978:76 [in key].

DIAGNOSIS.—*Helogenes uruyensis*, the most distinctive species in the family, can be distinguished from all other helogenids in having 32 to 37 anal-fin rays in contrast to 39 to 49 in the remainder of the family. The possession of 15 principal caudal fin rays, with eight principal rays on the lower lobe of the caudal fin, further distinguishes the species from *H. gouldingi* and *H. castaneus*, which have nine principal rays on the lower lobe of the fin and a total of 16 principal rays. *Helogenes uruyensis* is also separable from *H. castaneus* and *H. gouldingi* by a series of morphometric characters (see Table 2).

DESCRIPTION.—Morphometrics of the paratypes are given in Table 2.

Dorsal profile of body smooth, slightly convex from snout to dorsal portion of caudal peduncle. Ventral profile of body slightly convex from lower jaw to anus. Base of anal fin straight. Pectoral fin with seven rays, reaching to or falling slightly short of vertical through insertion of pelvic fin. Pelvic fin with six rays, reaching to vertical through insertion of second or third anal-fin rays. Anal-fin margin slightly convex anteriorly, concave posteriorly. Anal-fin rays 32 to 37. Rayed dorsal fin small, with five rays. Adipose dorsal fin present in all specimens examined.

Premaxilla with two rows of teeth, inner smaller, largely covered by fleshy lining of mouth. Lower jaw with a cardi-form band of teeth, outer row enlarged.

Anterior and posterior nares well separated, anterior tubular. Maxillary barbel extending posteriorly to slightly beyond vertical through insertion of pectoral fin. Medial and lateral mandibular barbels of same length or medial barbel slightly longer; medial barbel extending posteriorly to vertical through line approximately two-thirds along length of pectoral fin.

Five vertebrae in anterior vertebral complex; free vertebrae posterior to complex 38 (1), 39 (6).

COLORATION.—Overall coloration of head and body brown, somewhat mottled. Dorsal portions of head and nape somewhat darker. A series of unpigmented spots along lateral line; spots more numerous anteriorly, nearly contiguous in that region. Dark body pigmentation extending onto anterior one-third of caudal fin rays; posterior border of dark pigmentation on caudal fin discrete, with somewhat irregular margin.

Rayed dorsal fin mottled, somewhat darker basally. Adipose fin mottled, with hyaline border. Caudal fin dark on basal one-third, mottled on posterior two-thirds, borders hyaline. Anal fin dark brown on fleshy basal portion, mot-

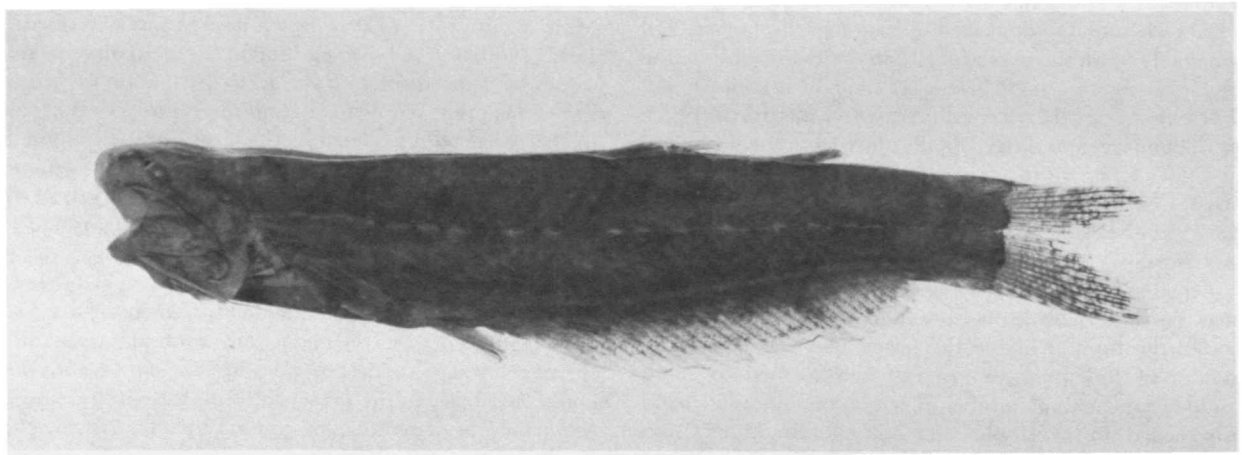


FIGURE 6.—*Helogenes uruyensis*, paratype, USNM 219598, 43.1 mm SL; Río Uruyén, Venezuela.

tled along medial one-third, distal one-third of fin hyaline. Pectoral and pelvic fins mottled basally, hyaline distally.

DISTRIBUTION.—Known only from the type-locality, the Río Uruyén, which flows from the southeast of Auyantepui in Guayana, Venezuela (Figure 4). The Río Uruyén is part of the Río Caroní system, a southern tributary of the Río Orinoco. The map in Glodek and Carter (1978, fig. 2) incorrectly indicates the locality as being in the Río Cuyuni system, a tributary of the Essequibo River.

REMARKS.—The original type series of *Helogenes uruyensis* consisted of the holotype and nine paratypes divided between the personal collection of Augustín Fernández-Yépez and MBUCV. Portions of Fernández-Yépez's personal collection were later transferred to the Ministerio de Agricultura y Cria (MAC) and subsequently to MBUCV. Although all paratypes are accounted for (see "Material Examined"), the holotype, a 49.5 mm SL specimen originally deposited in the personal collection (AFY 56613), was not located in the MBUCV holdings.

Fernández-Yépez in his description of *Helogenes uruyensis* recognized it as a subspecies of *H. marmoratus* Günther. *Helogenes marmoratus uruyensis* was distinguished by Fernández-Yépez (1967:170) from *H. marmoratus marmoratus* by differences in the length of the maxillary and mandibular barbels, anal-fin base length and anal-fin ray count. Although the two forms actually overlap in the lengths of the medial mandibular barbel (Table 2), lateral mandibular and maxillary barbels, and anal-fin base (Table 2), they do differ in anal-fin ray counts (Table 3). Fernández-Yépez's recognition of his form as a subspecies rather than as a species was evidently a consequence of what he thought to be close similarity in anal-fin ray counts in the two forms (anal-fin rays reported by Fernández-Yépez as being 37 to 41 in *H. marmoratus marmoratus* and 31 to 36 in *H. marmoratus uruyensis*). Results of this study have shown that *H. marmoratus* has rather 39 to 48 anal-fin rays. The distinctly lower count for that species reported by Fernández-Yépez appears to have been based on Eigenmann (1912:208), who listed his material from the Essequibo system as having 37 to 40 anal-fin rays, perhaps as a consequence of his failure to detect the very small anterior two rays. Re-examination of portions of Eigenmann's material along with other material from Guyana has failed to reveal any specimens of *H. marmoratus* with less than 39 anal-fin rays. Given the gap in anal-fin ray counts between Fernández-Yépez's *Helogenes marmoratus uruyensis* (32 to 37 based on our examination) and *Helogenes marmoratus* (39 to 48), we recognize the former as a distinct species, *Helogenes uruyensis*.

MATERIAL EXAMINED.—9 specimens (7, 36.5–43.1 mm SL).

VENEZUELA. Bolívar: Río Uruyén, south side of Auyantepui, USNM 219598, 1 (43.1, paratype of *Helogenes marmoratus uruyensis* Fernández-Yépez; formerly MBUCV V-2615, in part); MBUCV V-2615, 3 (36.65–40.0, paratypes of *H. m. uruyensis*); MBUCV V-10852, 5 (3, 36.5–39.6, paratypes

of *H. m. uruyensis*, formerly MAC 56028 and AFY 56614; anal-ray counts, but no other data taken from 2 other specimens.

Helogenes marmoratus Günther

FIGURES 7–9

Helogenes marmoratus Günther, 1863:443 [type-locality: Guiana (= Guyana)]; 1864:66 [expansion of species description, British Guiana (= Guyana); Essequibo River].—Eigenmann and Eigenmann, 1888:120 [citation]; 1890:312 [description based on Günther, 1864]; 1891:35 [citation].—Eigenmann, 1910:398 [citation]; 1912:207, pl. 22: fig. 2 [designation as type of family Helogeneidae (= Helogenidae); British Guiana (= Guyana): Aruataima, Holmia, Potaro Highland, Tukeit Landing].—Steindachner, 1915:86, pl. 11: fig. 6 [Brazil: Pará, Santarem, Rio Branco at Conceição; Surinam: Albina].—Fowler, 1915:228 [British Guiana: Holmia].—Jordan, 1923:150 [citation].—Gosline, 1945:53 [citation].—Van der Stigchel, 1947:109 [British Guiana: Holmia].—Fowler, 1954:4 [literature compilation].—Hoedeman, 1952:X.30.31.76:1–2, fig. [popular account].—Boeseman, 1952:182 [Surinam: Bush Creek, Coppename River]; 1953:9 [Surinam: Nassau Mountains, Morawini Basin, Zanderij].—Hoedeman, 1953:253 [photo; aquarium notes]; 1954:244–245, fig. 180 [popular account].—Boeseman, 1954:20 [Surinam: Paramaribo].—Hoedeman, 1959:244–245 [popular account]; 1968:141–142 [popular account].—McAllister, 1968:76 [branchiostegal rays].—Chardon, 1968:152 [Weberian Apparatus morphology].—Lundberg and Baskin, 1969:14, 17, 41, fig. 7, table 1 [caudal skeleton anatomy].—Hoedeman, 1974:388 [aquarium care, behavior].—Lundberg, 1975:70 [cranial morphology].—Glodek and Carter, 1978:76, 79 [in key, distribution].—Mees, 1983:56 [French Guiana: Mena River, Crique St. Anne; Crique Vampire; comments on species distribution].—Ortega and Vari, 1986:16 [Peru: Amazon basin].

Helogenes amazonae Delsman, 1941:80 [type-locality: Brazil: Manaus (= Manaus)].—Glodek and Carter, 1978:77, 80 [in key, distribution]. [New synonymy.]

Helogenes unidorsalis Glodek and Carter, 1978:75, fig. 1 [type-locality: Ecuador, Río Bobonaza between Sarayacu and Montalvo]. [New synonymy.]

DIAGNOSIS.—The possession of nine principal fin rays in the lower lobe of the caudal fin of *Helogenes marmoratus* distinguishes the species from *H. gouldingi* and *H. castaneus*, which have eight principal rays on the lower lobe of that fin. The 39 to 48 anal-fin rays of *H. marmoratus* separates that species from *H. uruyensis*, which has 32 to 37 anal-fin rays.

DESCRIPTION.—Morphometrics of the lectotype and measured non-type specimens given in Table 2.

Dorsal profile of body smooth, slightly convex from snout to dorsal portion of caudal peduncle. Ventral profile of body slightly convex from lower jaw to anus. Base of anal fin straight or very slightly sigmoid. Pectoral fin with seven rays, reaching beyond vertical through insertion of pelvic fin, sometimes to vertical through origin of anal fin. Pelvic fin with six rays, reaching posteriorly to region bordered by vertical through origin of anal fin and vertical through insertion of fourth anal ray. Anal-fin margin straight or slightly convex anteriorly, concave posteriorly. Anal-fin rays 40 to 48 [41] (see Table 3 relative to geographic variation). Rayed dorsal fin small, with five rays. Adipose dorsal fin

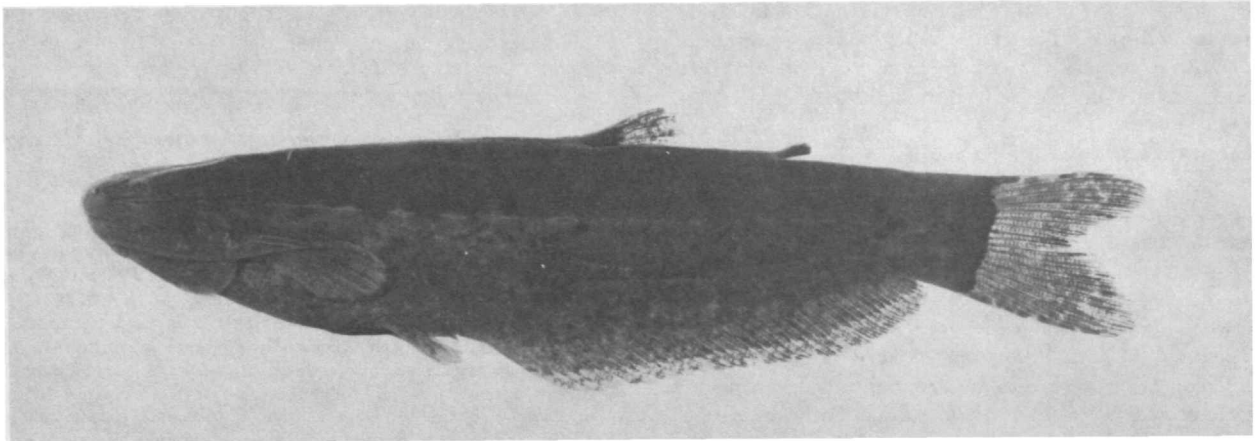


FIGURE 7.—*Helogenes marmoratus*, USNM 273057, 63.7 mm SL; Potaro River, Guyana.

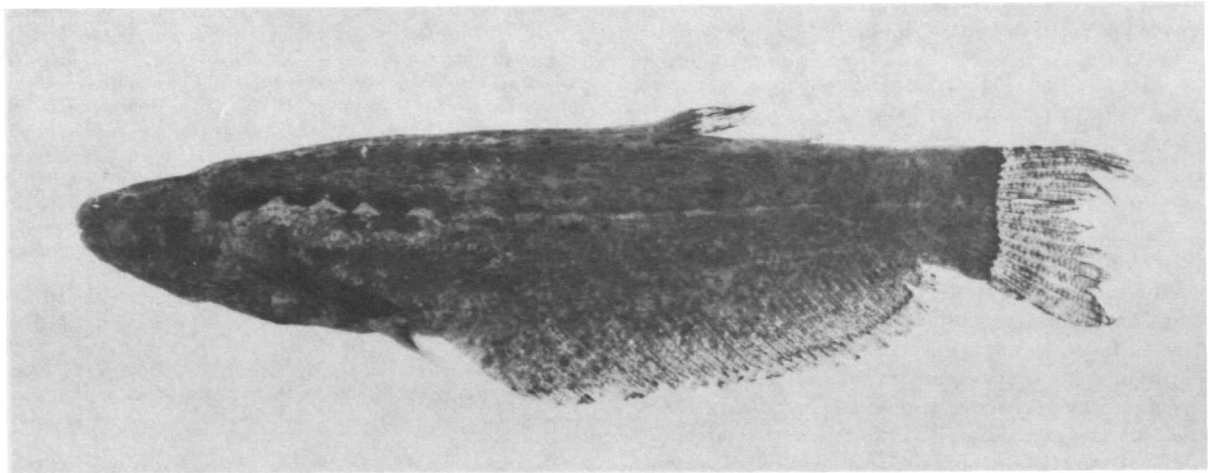


FIGURE 8.—*Helogenes marmoratus*, USNM 264030, 62.3 mm SL; Rio Tambopata, Peru.

present or absent [present in lectotype], when present demonstrating differing degrees of relative development.

Premaxilla with two rows of teeth, inner series smaller, sometimes difficult to locate in fleshy lining of mouth. Lower jaw with a cardiform band of teeth, outer row enlarged.

Anterior and posterior nares well separated, tubular. Maxillary barbel of variable length, typically extending posteriorly to beyond vertical through pectoral fin insertion. Medial mandibular barbel longer than lateral, developed to different degrees, extending posteriorly to region bordered by vertical through posterior of head and vertical through origin of anal fin.

Five vertebrae in anterior vertebral complex; free vertebrae posterior to complex 36 (5), 37 (26), 38 (61), 39 (24), 40 (2).

COLORATION.—Overall pigmentation of head and body

dark, mottled to different degrees. Some individuals with horizontal stripe of darker pigmentation extending from rear of head along lateral line; stripe extending up to one-third distance along lateral line. Rotund or horizontally elongate spots of light pigmentation distributed along lateral line, particularly on anterior portion of body where they are nearly contiguous. Specimens from Essequibo River with uniform dark pigmentation along middorsal portion of body and proximate regions. Individuals from other portions of species range with a variably intense dark middorsal stripe that extends from rear of head to insertion of dorsal fin. Middorsal stripe paralleled on each side by stripe that extends from head to meet its counterpart proximate to adipose fin. Dark body pigmentation extending onto base of caudal fin, posterior margin of dark coloration discrete; border ranging from straight to wavy.

Pectoral fin mottled in juveniles, particularly basally;



FIGURE 9.—Geographic distribution of *Helogenes marmoratus* (solid circles indicate localities of material examined; stars indicate literature records; some symbols represent more than one collecting locality or lot of specimens).

more uniformly pigmented in adults, often dark brown. Anal fin dark basally in juveniles, mottled distally; more uniformly dark in adults. Anal-fin margin hyaline in specimens from Guianas and upper Río Orinoco, pigmented in individuals from Amazon, with a thin darker line of differing degrees of intensity paralleling distal margin of fin approximately one-fifth of distance from fin margin. Rayed dorsal fin dark basally in juveniles, uniformly dark in adults, sometimes with tip or margin hyaline. Adipose fin mottled in smaller individuals, dark in larger specimens. Caudal fin dark on basal one-third, mottled on posterior portion; degree of posterior mottling and extent of development of pigmentation correlated with overall intensity of body coloration.

DISTRIBUTION.—Atlantic drainages of Guyana, Surinam, and French Guiana, upper Río Orinoco and Río Negro systems in Venezuela, Amazon basin in Brazil, Peru, and Ecuador (Figure 9).

ECOLOGY.—Collections of *Helogenes marmoratus* in the Corantijn River system of Surinam, tributaries of the upper Río Orinoco and upper Río Negro in Venezuela, and in the Río Tambopata of the Río Madeira system in southeastern Peru indicate that the species is typically an inhabitant of black or clear waters, usually in forest streams with moderate to swift current flow over firm sand or gravel bottoms. The only exception, one sample from Surinam (USNM 226152), was taken in an artificially impounded black water pond with slow current. In rain-forest streams under more open canopy, with a resultant greater degree of light pen-

etration, *Helogenes marmoratus* is typically found in clumps of aquatic vegetation, whereas in well-shaded sites lacking submerged or emergent aquatic vegetation, it has been collected in leaf litter and debris.

Examination of the stomach contents of specimens from Peru, Venezuela, and Surinam has shown that the species feeds evidently exclusively on allochthonous terrestrial insects, particularly ants, which presumably are blown or fall onto the water surface.

VARIATION.—*Helogenes marmoratus* is the most geographically wide-ranging species recognized in this study, with examined specimens originating in the vast expanse from the Atlantic drainages of the Guianas to the upper Río Orinoco, to a number of localities along the main stream of the Amazon and some of its major tributaries, including the Río Madeira, Río Tapajós, Río Negro, Río Ucayali, and Río Marañón systems (Figure 9). These relatively small fishes evidently live in discrete populations that are apparently limited to smaller tributaries.

The species shows a significant amount of meristic, morphometric, and coloration variability across its range, a situation that is to be expected given the broad geographic expanse involved and apparently somewhat disjunct distribution of the species in black or clearwater tributary streams rather than main rivers and whitewaters. The degree of intraspecific morphometric variability in *H. marmoratus* is pronounced (Table 2), with the ranges of the relative distances from the snout to the dorsal-fin origin and between the rayed and adipose dorsal fins being notably broad.

However, these proportions show significant overlap when samples of the species from different areas are compared, and as such they do not serve to subdivide the species into less-inclusive subunits. Neither are any geographical clinal patterns obvious in these characters.

Among meristic characters, only the principal caudal-fin ray count, the number of vertebrae, and the anal-fin ray count show variability within the family. The first of these, the principal caudal-fin ray count, is constant within *Helogenes marmoratus*. Although that species shows variability in the number of vertebrae, the modal count for each population of the species is either 38 or 39, with large scale overlap in the ranges of the values for members of each population. That character does not show any recognizable geographic pattern within the available material of *H. marmoratus*. Anal-fin ray counts do show a distinct pattern (Table 3) although they do not serve to discretely subdivide the species. Specimens of *H. marmoratus* from the type region, the Essequibo River, have the lowest average number of rays (41.32). Individuals from Surinam and the Orinoco basin in Venezuela have higher average anal-fin ray counts (43.22 and 43.48 respectively). Those populations also have a greater range of anal-fin rays and higher maximum anal-fin ray counts. Specimens from the Rio Amazonas basin have yet higher average anal-fin ray counts (43.58–45.20) and further increases in the value of the lowest anal-fin ray count, most notably in the Ecuadorian and Peruvian samples.

As noted in the description of coloration, there is geographic variability in pigmentation along the dorsal surface of the body and on the anal fin. The form of the border between the hyaline or mottled posterior portion of the caudal fin and the dark pigmentation that extends from the body onto the base of the fin also varies somewhat. A straight demarcation is most common in the Guianas, but that border is typically extremely wavy in specimens from the upper Rio Orinoco. However, some individuals from the Guianas have irregular borders, and nearly straight borders are found in a few specimens from the Rio Orinoco system. Although some of the pigmentation differences appear to be geographically consistent and may delimit subunits of the species, we prefer not to recognize those groupings formally until more geographically inclusive collections of the species are available for further analysis.

REMARKS.—The original description of *Helogenes marmoratus* (Günther, 1863:443) was based on two specimens from the Essequibo River. One of these specimens was borrowed some years ago by another worker, but not returned, and must be presumed lost. The remaining individual (BMNH 1864.1.21:83, 56.8 mm SL) is designated herein as the lectotype of the species.

As discussed above, *Helogenes marmoratus* demonstrates variability both in the presence or absence of an adipose dorsal fin, and in the size of that fin when present. Refer-

ence to the description of *Helogenes unidorsalis* by Glodek and Carter (1978:77) and the accompanying key shows that the primary basis for the recognition of the species was the absence of the relatively small adipose fin, an uncertain character by which to delimit a species in light of the intrapopulation variability of the development of that structure in various species in the Ostariophysi.

The two other characters cited in Glodek and Carter's diagnosis of *Helogenes unidorsalis* are the possession by the species of 37 to 44 anal-fin rays and the presence of dark pigmentation on the pectoral fins. Another evidently diagnostic character for the species not commented on by those authors was their report of only six rays in the pectoral fin rather than the seven typical for helogenids. Examination of the available specimens of the type series of *H. unidorsalis* (FMNH 80463, 80464) has shown that there are rather 44 to 48 anal-fin rays in those individuals, a count that falls within the range of *H. marmoratus* (Table 3). Similarly the type series has a constant value of seven pectoral-fin rays in agreement with other helogenids and with the number of rays shown in the illustration of the holotype (Glodek and Carter, 1978, fig. 1). The degree of pectoral-fin pigmentation increases ontogenetically in all of the recognized helogenid species. Material of *H. marmoratus* from the Essequibo River, the type region for the species, has pectoral fins that range from hyaline with limited mottling in smaller specimens, through individuals with some pectoral fin pigmentation (e.g., Eigenmann, 1912, pl. 22: fig. 3), to larger fish that have dark fins such as those reported for *H. unidorsalis*. The specimens of *H. unidorsalis* are relatively large (59.4–73.0 mm SL) and appear to have been poorly preserved, with a consequent loss of pigmentation on the body, making the pectoral-fin coloration even more obvious. In light of the intrapopulation ontogenetic variability of the character, the large size of the specimens, and the presence of darkly pigmented pectoral fins in other helogenids, particularly larger individuals, that pigmentation character is not considered useful in delimiting *H. unidorsalis*.

None of the characters cited in the original description of *Helogenes unidorsalis* distinguish that species from *H. marmoratus*. Neither have differences between the nominal forms in other examined features been discovered during this study. As a consequence *H. unidorsalis* is herein considered a synonym of *H. marmoratus*.

Delsman, in his brief original description of *Helogenes amazonae* (1941:80), cited differences in anal-fin ray counts, pectoral-fin length, and the location of the abrupt terminus of the dark pigmentation that extends from the body onto the base of the caudal fin as separating his nominal form and *H. marmoratus* of Günther. *Helogenes marmoratus* was listed by Delsman as having 37 to 40 anal-fin rays contrary to the 45 of *H. amazonae*. The low anal-fin ray count cited for *H. marmoratus* was evidently taken from Eigenmann (1912:208), a publication Delsman cited relative to the

perceived differences in pigmentation. Examination of portions of Eigenmann's material along with other specimens from the Guianas has failed to reveal any *H. marmoratus* with fewer than 39 anal-fin rays. Günther, in his original description of the species, indicated that his material had 42 rays, and Steindachner (1915:87) lists 41 to 46 rays for Surinamese and Brazilian specimens of the species. Material examined during this study has 39 to 48 anal-fin rays, a range bracketing the count of 45 in the holotype of *H. amazonae*. The length of the pectoral fin and the position of the posterior termination of the dark pigmentation on the basal portion of the caudal fin in *H. amazonae* have similarly been found to fall within the ranges of those characters for *H. marmoratus*. None of the characters originally cited as separating *H. amazonae* from *H. marmoratus* distinguish the forms. Neither have any other features been found during this study to delimit the nominal species. *Helogenes amazonae* is consequently considered a synonym of *H. marmoratus*.

Glodek and Carter (1978:81) raised the question of whether the main stream of the Amazon might "act as a barrier to the dispersal of these fishes" (helogenids) to the southern portions of the Amazon basin. More recently Mees (1983:57) noted that because Steindachner (1915:86) had previously cited *Helogenes marmoratus* from Pará and Santarem along the southern banks of the Brazilian Amazon, such a hypothesis was invalid. We have also examined specimens captured in the Rio Cururú, a tributary of the Rio Tapajós, and have collected several series of individuals in the upper Rio Madeira system in southeastern Peru (Figure 9), with both areas being well south of the main Rio Amazonas. A second species (*H. gouldingi*), described in this paper from the middle Rio Madeira system, also occurs distinctly south of the main portion of the Rio Amazonas (Figure 4).

Material we examined of *Helogenes marmoratus* originated from the Atlantic drainages of Guyana, Surinam, and French Guiana, the Rio Tapajós, Pará, Santarem, and vicinity of Manaus in Brazil, northeastern and southeastern Peru, eastern Ecuador, and both the upper Rio Orinoco and upper Rio Negro in Venezuela. Within Brazil *H. marmoratus* was also reported by Steindachner (1915:86) from the Rio Branco near Conceição (Figure 9).

MATERIAL EXAMINED.—312 specimens (99, 19.75–73.0 mm SL).

BRAZIL. *Amazonas*: Manaus, BMNH 1913.3.6:28-29, 1 (39.65); IRSNB 545, 1 (58.15, holotype of *Helogenes amazonae* Delsman). Manaus, Reserve Ducke, IRSNB 19647, 1 (61.5). Turbinengraben, FMNH 70206, 1 (19.75; locality uncertain). *Pará*: Mission, Rio Cururú (probably mission franciscaine du Cururú, cited by Collette, 1982:737), FMNH 70114, 1 (33.7); FMNH 70115, 6 (4, 36.3–45.2). Santarem, NMW 46356, 7; NMW 46357, 1. Santarem, Uruará "brook" into Rio Amazonas, CAS 45776, 2 (30.65–

31.2). Lema, Rio Bem Fica (site could not located), NMW 46353, 14; NMW 46355, 1.

ECUADOR. *Pastaza*: Río Bobonaza, between Sarayacu and Montalvo, FMNH 80463, 1 (73.0, holotype of *Helogenes unidorsalis* Glodek and Carter); FMNH 80464, 4 (59.4–67.4, paratypes of *H. unidorsalis*; two of original six paratypes were not available for examination).

PERU. *Madre de Dios*: Reserva Natural de Tambopata, between Río Tambopata and Río La Torre, small forest stream draining into Río Tambopata, USNM 264030, 19 (39.3–62.3); USM 1595, 4 (42.6–56.8); USM 1596, 5 (31.25–64.5). *Loreto*: Río Ucayali basin, forest stream at right bank of Río Carahuayte, about 35 km SE of Jenaro Herrera (04°55'S, 73°40'W), ZMA 116.987, 3. Río Ucayali basin, affluent of Río Copal, 15 km from Jenaro Herrera on road to Colonia Angamos (04°55'S, 73°40'W), ZMA 116.979, 1.

GUYANA. Essequibo River, BMNH 1864.1.21:83, 1 (56.8, lectotype of *Helogenes marmoratus* Günther). *Essequibo*: Holmia, AMNH 7113, 2 (49.4–57.45). Upper Potaro River, Aruataima Falls, AMNH 27690, 1 (55.1); NMW 46359, 1. Upper Potaro River, AMNH 27689, 2 (36.75–55.75); USNM 273057, 10 (8, 21.0–63.7); ZMA 110.718, 1; BMNH 1911.10.31:99-101, 2; NMW 46354, 1. Potaro River, Kaieteur, BMNH 1972.10.17:693-732, 37. Georgetown, Kurupung River, AMNH 8224, 1 (32.4). Essequibo River, Morabelli, above Bartica, BMNH 1972.10.17:753-804, 19 (7, 25.0–71.5).

SURINAM. No exact locality, NMW 46358, 2. *Nickerie District*: Stream entering Corantijn River 2 km downstream of Cow Falls, USNM 226149, 4 (25.45–47.1). Stream draining into Corantijn River at Mataway, USNM 226150, 7 (6, 21.7–63.0). Kamp Creek where crossed by road to Lucie River, USNM 226151, 1 (39.25). Stream at Kamp Infrastructure, USNM 226152, 4 (2, 35.45–39.0). Stream draining into Kabalebo River near Kamp Anjoemara, USNM 226153, 4 (22.7–61.7). Tributary to Sisa Kreek downstream of where Sisa Kreek is crossed by road to Lucie River, USNM 226154, 1 (32.1). Stream draining into Nickerie River, 12.5 km SW of Stondansie Falls, ZMA 105.828, 1. *Para District*: Carolina Kreek, approximately 10 km SE of Zanderij, ZMA 106.531, 68. *Saramaca District*: Tributary to Saramaca River (03°52'W, 56°55'W), ZMA 106.538, 1. *Brokopondo District*: Tapoeripa Kreek near Hermansdorp, ZMA 106.532, 3. Tapoeripa Kreek, approximately 5 km from Bronsweg, ZMA 106.533, 2. Tapoeripa Kreek near Brokopondo, ZMA 106.534, 3. Dabikwen Kreek, approximately 5 km from Afobaka, ZMA 106.535, 2. *Marowijne District*: Maka Kreek, 10 km S of Stoelmans Island, ZMA 106.536, 3. Stream draining into Morawijne River 36 km N of Stoelmans Island, ZMA 106.537, 3.

FRENCH GUIANA. *Cayenne*: Oyapock River basin, Yawapa Creek near Trois Sauts (02°15'N, 52°53'W), ZMA 107.824, 1. Crique Balaté, affluent to lower Maroni River,

10 km SSE of St. Laurent (05°26'N, 54°02'W), ZMA 116.893, 10.

VENEZUELA. *Territorio Federal Amazonas*: Pozo de Lucas, tributary of Río Orinoco, 7 km from San Fernando de Atabapo, MBUCV V-12989, 4 (32.1–58.4). Upper Río Orinoco, Burned Mountain Creek (in vicinity of Mount Duida, see LaMonte 1929:1), AMNH 9626, 3 (47.9–60.7). Stream draining into Río Orinoco, where crossed by high-

way from Puerto Ayacucho to Samariapo, 25 km S of Puerto Ayacucho, USNM 269975, 14 (10, 24.7–43.3). Park along road from Puerto Ayacucho to Samariapo, 3 km S of Puerto Ayacucho, FMNH 83867, 4. Stream 32 km S of Puerto Ayacucho where crossed by road from Puerto Ayacucho to Samariapo, FMNH 83868, 13 (2 specimens cleared and stained). Río Mawarinuma, 5 km above Cerro de la Neblina base camp (0°55'N, 66°10'W), AMNH 56096, 1.

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